On compromise in foraging and an experiment by Krebs et al. (1977)

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Abstract. A vectorized version of the method of stochastic dynamic programming is used to demonstrate that behaviour observed in Parus major by Krebs et al. (1977) is more consistent with the hypothesis that animals compromise between time and energy in foraging than with the hypothesis that they maximize their rate of energy gain.

Key words: Foraging — Behavioral ecology — Vector optimization — Dynamic programming

1. Introduction

This article has two objectives, one general, one specific. On the one hand, the article’s general purpose is to demonstrate a methodology that enables merely qualitative knowledge about the way in which an animal’s physiological and environmental conditions affect its fitness to generate quantitatively testable predictions about its behaviour. On the other hand, the specific purpose of the article is to demonstrate that behaviour observed in the great tit, Parus major, by Krebs et al. (1977) is more consistent with the hypothesis that animals compromise between time and energy in selecting prey than with the hypothesis that they maximize rate of energy gain. We begin here with the general objective; we turn to the specific objective in Sect. 3. Both the advantages and the limitations of the methodology are discussed in Sect. 5.

Recent work by McNamara and Houston (1986) and Mangel and Clark (1986) has provided a unified theory for modelling behaviour in terms of its evolutionary advantage. This theory is concerned with costs and benefits to an animal’s fitness of decisions taken throughout an entire interval, say [0, T_{max}]. Modelling the relationship between such decisions and the animal’s fitness is achieved in two stages. First, it is assumed that relevant aspects of the animal’s state at any time, whether physiological or environmental, can be described by defining a vector of decision-dependent random variables; this vector is called the animal’s state vector, or simply state. Second, the animal’s long-time contribution to the gene pool is related to its state at the end of [0, T_{max}], say Y, by defining a fitness function, f. Thus f = f(Y). But Y depends on the sequence of decisions taken...
by the animal during \([0, T_{\text{max}}]\), which we shall call its policy, and denote by \(\pi\).
Thus \(Y = Y(\pi)\). Then the animal's fitness is measured by the random variable
\(f(Y(\pi))\); and the policy \(\pi^*\) that maximizes its expected value can be determined
by stochastic dynamic programming. If the animal is maximizing fitness, then
the computed policy should correspond to its observed behaviour. Henceforward,
we will refer to this unified theory as DFT (for dynamic foraging theory). For a
recent review of DFT, see Houston et al. (1988).

In principle, this theory is capable of assessing trade-offs between conflicting
objectives by measuring the cost of each feasible action in terms of the common
currency \(E[f(Y)]\), where \(E\) denotes expected value. In practice, however, there
remains the difficulty of defining a suitable fitness function. Consider, for example,
an animal that must decide between feeding and using its time for other activities
affecting its future reproductive success, e.g. defending its territory; and suppose
that \([0, T_{\text{max}}]\) is the predetermined interval during which all activities must happen
(perhaps daylight hours, or an intertidal period). Let \(\Phi\) be the amount of energy
ingested during \([0, T_{\text{max}}]\) and let \(T_{\text{max}} - \Psi\) be the time required to obtain it, so
that \(\Psi\) is the time allotted to the other activities; both \(\Phi\) and \(\Psi\) are random
variables. Then fitness is an increasing function of \(\Phi\) and \(\Psi\). Thus we have
qualitative information about \(f\). But any direct application of DFT would require
the relationship between \(\Phi, \Psi\) and future reproductive success to be defined
explicitly; and this, at the very least, would require a very complicated model.

With this in mind, we explore in this paper a variant of DFT, recently suggested
by Mesterton-Gibbons (1988), which is applicable whenever the vector \(Y\) can
be defined so as to satisfy three fundamental conditions. The first is that if
\(Y = (Y_1, \ldots, Y_m)\) has \(m\) components then, for \(k = 1, \ldots, m\), the random variable
\(Y_k\) is dimensionless and takes values between 0 and 1, with 0 corresponding to
the worst possible value of \(Y_k\) (from the viewpoint of future reproductive success)
and 1 corresponding to the best. In practice, this will be achieved by scaling
physiological and environmental variables with respect to their predetermined
natural capacities, so that each \(Y_k\) is a kind of merit function for the \(k\)th variable.
The second fundamental condition is that fitness be an increasing function of
each component of \(Y\), i.e. for \(k = 1, \ldots, m\), \(\partial f / \partial Y_k > 0\) whenever \(0 < Y_k < 1\). Then
the rationale behind the aforementioned variant of DFT is that if \(Y_1, \ldots, Y_m\)
were determinate then, because \(f\) is an increasing function of each of these
variables, fitness would be maximized by the policy \(\pi\) that made
\(Y_1(\pi), \ldots, Y_m(\pi)\) as large as possible, subject to constraints on decisions made
during \([0, T_{\text{max}}]\); but, because \(Y_1(\pi), \ldots, Y_m(\pi)\) are random variables, their
expected values are optimized instead. Thus, in the absence of an explicit
expression for fitness, the optimization of \(E[Y_1(\pi)], \ldots, E[Y_m(\pi)]\) is substituted
for the optimization of \(E[f(Y(\pi))]\). Clearly, because the sequence of decisions
that would maximize \(E[Y_k(\pi)]\) will not simultaneously maximize
\(E[Y_1(\pi)], \ldots, E[Y_{k-1}(\pi)], E[Y_{k+1}(\pi)], \ldots, E[Y_m(\pi)]\) for \(k = 1, \ldots, m\), a com-
promise must be sought among these objectives.

Following Salukvadze (1979), for any instant during \([0, T_{\text{max}}]\) we can define
an optimal compromise as follows. Let \(E[Y_1], \ldots, E[Y_m]\) be known as currencies,
let the \(m\)-dimensional vector space in which \((E[Y_1], \ldots, E[Y_m])\) is a typical
point be known as currency space, and let \(U_k\) be the maximum feasible value of